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Arachis hypogaea L.*

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(PLATES 83-85.) *

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History.

The study of this plant was undertaken for the purpose of discovering, if possible, some additional facts concerning its habit of ripening fruit under ground. Other species of the Leguminosae are known to share this peculiarity with *Arachis*. Among the best known of these are *Vicia amphicarpa* and *Trifolium subterraneum*. *Vicia amphicarpa* bears two kinds of flowers and accordingly two forms of fruit, only one of which is developed under ground. The flower which gives rise to this fruit is formed and always remains underground. The other form of flower and fruit is developed normally, so that in this case the peculiarity of the plant lies as much in its underground flower as in its underground fruit, as the latter seems to be a natural sequence of the former.

Trifolium subterraneum bears but one kind of flowers. These are developed in heads. After flowering, the peduncle bearing the head sinks to the ground and, continuing to lengthen, pushes the head under the soil. The seeds will ripen above ground, and, according to Belli, if the heads are prevented from going into the earth, the seeds germinate easily if the integument is broken; otherwise the germination takes place with difficulty.

Differing essentially from both of these, *Arachis hypogaea* has but one form of flower which is sessile and remains so. It is a growth from the base of the ovary itself which is prolonged until the ovary is pushed into the ground. This growth is technically known as a gynophore. Ovaries which are hindered by any circumstance from reaching the ground do not produce fruit.

Seven species of *Arachis* are now recognized. These are: *A. pusilla*, *A. prostrata*, *A. villosa*, *A. glabrata*, *A. marginata*, *A. tuberosa* and *Arachis hypogaea*, all perennial with the exceptions of *A. hypogaea* and *A. pusilla*. Of these species six are found only in Brazil. The remaining one, *Arachis hypogaea* is cultivated at the present time throughout the warmer regions of the globe.

Little is known with certainty concerning the earlier history of *Arachis*. The fact that all but one of its species are confined to Brazil would seem an indication that it is a native of that country, and in fact De Candolle ascribes its origin to that place. Other authors think it to be a native of Africa, as its importance there as food is so great and its cultivation so general. Still others hold the opinion that it has a Japanese or Chinese origin. Opposing this opinion are the facts that no allusion is made to this plant in the older literature of those countries and that the fruit is not produced there in any great quantities.

Sloan, writing in the latter part of the sixteenth century, speaks of it as having been carried to the West Indies from Guinea in slave ships as food for the slaves, and says it was taken to Guinea from Peru. Oviedo, writing in 1547, describes *Arachis* under the name Mani and states that it is very common in the gardens of the West Indies. From the name Mani is derived the name which the plant now bears in Cuba, Mandubi or Mandobi. Jean de Lery, in 1578, writing a history of travel in Brazil, speaks of *Arachis* as Manobi. The author of the *Noticia do Brasil* (1589) speaks of the plant under the name Amandao (large Mandel). Rumph described the plant, giving it the name *Chamaebalanus Japonicus*. Parkinson, writing about 1648, described the American *Arachis* and called it *Arachis hypogais Americanus*.

It is estimated that the yearly production of peanuts in this country is about 4,000,000 bushels and that this constitutes about one-sixth of the production of the entire world. This amount is con-

tributed almost entirely by Virginia, Georgia, Tennessee and North Carolina, Virginia ranking first in its production. Notwithstanding this large amount supplied to our market and the high nutritious value of the seed, the peanut is nowhere used in the United States as an article of food—as it is used in other countries. Some effort has been made, however, to show how valuable it would prove if so utilized. In Germany experiments have been made with reference to adopting it as an article of diet for the army; and it is said to be already in use there as a dietetic treatment for diabetes.

The following analysis is taken from statistics furnished by German authorities and will serve to show what valuable properties it possesses as a food constituent:

Water, . . .	7.85	Fibre, . . .	4.29
Ash, . . .	2.77	Fat, . . .	49.20
Protein, . . .	29.47	Nitrogen, . . .	4.67

The oil of this fruit is used as a substitute for olive oil, which it much resembles, and to which it is even sometimes preferred. It is also used as a lubricant and in the manufacturing of toilet soap.

Notwithstanding the fact that the fruit of *Arachis* formed so important an article of commerce and that, on account of its utilitarian value, it was so widely cultivated, it has been correctly described only in comparatively recent times.

Piso, writing in 1658, says only of the flower that it is small and yellow, and states that the fruit originates on the root-fibres. The later botanists up to the year 1805 all described the structure of the flower erroneously. The long stem-like calyx was assumed to be a flower stalk even by those botanists who had access to the living plants. In 1805 Poiteau published the first correct description of the structure of the flower. Robert Brown afterward confirmed Poiteau's description in the appendix to Tuckey's Narration of an Expedition to the Zaire, in 1816. Notwithstanding the work of Poiteau, Bentham as late as 1839 writes of *Arachis* as a plant with dimorphous flowers. One form, with calyx and corolla, which are always sterile, the fertile flowers having "neither calyx, corolla nor stamens, but from between two bracteolae, similar to those which are found at the base of the sterile flowers proceeds a stiff rigid stipe or torus, which is speedily reflexed and elongated,

and is terminated by what appears to the naked eye a short point. Examined under a glass this point discloses at its extremity a truncated, somewhat concave and dilated stigma."

Hugh M. Neisler, acting upon the supposition that Bentham's statements were correct, made some observations upon the fructification of *Arachis* which convinced him that, in his own words, "The flowers of *Arachis* are all petal-bearing and all fertile." (Silliman's Am. Journal of Science and Art, 2d series, 19: 1855). Bentham remained unconvinced and published a reply in Hooker's Journal of Botany and Kew Garden Miscellany, 7: 1855. It is difficult to understand how Bentham could have persisted in his mistake, as he did, in the face of so much evidence.

It requires no very expert examination of the plant to be convinced that what he mistook for a cleistogamic flower is the naked ovary after the flower parts have fallen away; and that what he describes as the sessile stigma of the barren ovary is the scar left by the deciduous style.

As to the affinities of *Arachis* no satisfactory conclusion is yet attained. Linnaeus placed it next to *Cicer*; Persoon, nearer *Anthyllis*; Jussieu, between *Ononis* and *Anthyllis*. De Candolle, classifying it according to the character of its embryo, place it among his *Geoffroyae*, but at the same time recognizing how little it conforms in other respects to these plants, suggested its forming together with *Voandzeia* a distinct tribe. Robert Brown says that *Arachis* and *Cercis* possess straight embryos in common with the Caesalpinieae and Mimoseae and in which respect they differ from all of the Papilionaceae. Bentham, adhering to his opinion that *Arachis* possessed dimorphous flowers, points out a resemblance to *Stylosanthes*, but finds an important difference from the group Hedysareae, of which *Stylosanthes* is a member, in the unarticulated legume. He finds *Arachis* not at all similar to *Voandzeia*. Pending a harmonizing of these conflicting opinions *Arachis* is usually accepted among the Papilionaceae.

General Description of the Plant.

Arachis hypogaea is a low annual plant, with one upright flowerless branch surrounded by decumbent spreading branches, upon which the flowers are borne. The stem is cylindrical and smooth,

at the base becoming angular and slightly hairy above. The leaves are alternate and pinnate with two pairs of nearly sessile leaflets, the inferior pair of which are nearly elliptical and the superior pair are cuneate and noticeably larger. The leaflets are furnished with pulvini which comprise the entire stalklet (about 1 mm. in length). The primary petiole is also furnished with a pulvinus and with two adnate stipules which partly clasp the stem. The straight tap root gives off numerous lateral roots.

Nearly all of the roots examined bore quantities of the small tuber-like swellings which are a much discussed characteristic of the roots of the Leguminosae. These occur indifferently on the main and lateral roots.

The flowers develop in the axils of the leaves. They are sessile, but with a long calyx, which may easily be mistaken for a peduncle. This calyx varies from 3 to 14 mm. in length, is cylindrical, two-lipped, hairy and with two bracts at its base. The upper lip is two-toothed. The corolla is papilionaceous and yellow. The stamens are monadelphous and inserted in the calyx. They are ten in number and of two kinds, one with long two-celled anthers dehiscing laterally, and one with nearly spherical one-celled anthers.

The ovary is superior, small, conical and one-celled. The style is inserted a little to one side of the apex of the ovary. It is long, cylindrical, exceedingly slender, hairy for a short distance along one side from the stigma, and is terminated by a flat stigmatic surface. After fertilization the gynophore begins its growth. The flower parts fall off; sometimes the style may be seen as a brown hair-like appendage to the ovary after the flower falls. More frequently it is thrown off with the flower. The ovary becomes tipped with a hardened and brown point. The gynophore curves so that it points towards the earth. The growth of the gynophore continues until the ovary has penetrated the earth for some distance. The ovary then begins to swell to form the pod. The part of the gynophore under ground thickens and develops hairs from its epidermal cells which are in every way similar to root hairs.

The fruit develops only under ground. It is a one-celled pod bearing from one to three, or according to Kurtz, sometimes as many as seven seeds. The number is usually two. The pod is inde-

hiscent. The seeds have a purplish brown membrane and no albumen. The embryo is straight. The large, fleshy cotyledons are furnished with pulvini and are exceedingly rich in oil.

General Observations on the Plants Studied.

The following study was made with plants raised during two successive summers in Englewood, N. J.; Lawrence, L. I., and in Potsdam and Buffalo, N. Y. In New Jersey and on Long Island the plants thrived and produced fruit. The seeds planted in richer soil in northern New York produced healthy looking, well-grown plants with flowers but no fruit developed. The plants grow best in a dry sandy soil, and a warm, at least temperate, climate. Under favorable conditions of weather fruit was obtained from seeds planted in Lawrence within two months. From two to three months is usually required. Plants of a crop raised in Lawrence when pulled up during the early part of October were found to bear a quantity of tubers on their roots. On other plants of the same crop examined in November no tubers were found.

In the nyctotropic movement of the leaves, which has already been described by Darwin in his "Power of Movement in Plants," the main petiole sinks downward; the leaflets twist downward and backward so that the lower surfaces of each pair are applied to each other. In this position they form a little packet shutting around the petiole, with the superior pair closed over the inferior and the tips pointing upward. The leaves vary their positions on the stem during the day in such a way as to keep their upper surfaces inclined toward the sun. When a leaf was separated from the stem so that the water supply was cut off while evaporation was going on it was discovered that the loss of water made itself apparent first in the upper half of the pulvinus of the leaflets.

When cut at night or at four p. m. the movement was quicker, probably because the water in the cells of the upper half of the pulvini had already begun to lessen in quantity. The leaves of some stems cut in the morning slept after about one-half hour; others slept at once. The leaves of stems cut on a hot day slept more quickly than those cut on a cool day; those cut at about four in the afternoon more quickly than those cut in the morning.

As the growth of the gynophore is solely for the purpose of pushing the ovary into the soil, its length is determined entirely by the distance of the flower from the ground. The gynophores in the axils of the lower leaves are much shorter than those above, as they reach the ground sooner; for the same reason the gynophores on the more decumbent branches are shorter than those on the more erect. Gynophores bearing fruit have been seen as short as five millimeters; they vary from that length to fifteen or sixteen centimeters, according to their position on the branch and the position of the branch in relation to the ground. That the only condition regulating the length of the gynophore is the distance of the ovary from the ground, was illustrated by the following fact:

One of the plants in a row was entirely removed, together with a portion of the earth about the roots, leaving a hole somewhat more than a foot in depth. A gynophore of a neighboring plant had grown down to the ground at this place and already attained a maximum length. As the ground around it was taken away, it was found after several days still growing down into the darkness and seeking the soil.

The angle which the gynophore forms with the stem is determined by the position of the stem. Accordingly it varies from a right to an acute angle, as the stem runs parallel with the ground or is inclined to an upright position.

The hairs are formed as soon as the gynophore reaches the soil, as all of the underground portion is thickened and bears hairs.

The growth of the gynophore under ground before the fruit begins to form also varies considerably. In a case where three gynophores developed from one axil, the underground portion of the oldest was 24 mm. long, the next 30 mm. and the next 55 mm. This represents the usual relation.

Flowers have been observed on the subterranean portion of the stem. These were perfect and, with the exception of being etiolated, similar in all respects to those above ground. They without doubt produce fruit, as gynophores were also observed which had developed entirely under the ground. This fact, together with the one that the parts of the flower fall off almost as soon as they open, gives evidence that the flower is close fertilized. In the course of its growth the gynophore grows as nearly per-

pendicularly as possible, apparently obeying the same law as the main root.

When the fruit begins to develop, the growth of the gynophore ceases. The first intimation that the fruit is about to form is a very slight swelling in the lower part of the ovary. As it develops, growth takes place more rapidly on one side than the other, so that the fruit is turned to one side with its length parallel to the surface of the ground. The lower seed, that is the seed next to the base of the ovary, grows to some size before the other begins its growth. (There are seldom more than two.)

Seeds were also kept germinating in the laboratory in sawdust during the two years of study. It was observed that after the root had grown about from one to two mm. in length, the epidermis would break in a circular line around its entire circumference. This happened invariably. This line marks the limit between the root and hypocotyl, as is shown by the change in the bundles at this point from radial to collateral. As the primary root grows it soon develops rootlets which appear in four regular longitudinal rows at an equal distance from each other. Neither the rootlets nor main root bear root hairs. Their surface is roughened and of a yellowish color, both appearances being due to tissue which scales off, the cast-off tissue being decidedly yellow. The etiolated hypocotyl is thick and fleshy and often much curved in its efforts to extricate the cotyledons from the shell. It frequently narrows down to a thinner portion near the cotyledons which is green. This thickening of the etiolated portion of the hypocotyl is of special interest for the following reason: Experiments have shown that the rule for stems growing in darkness is an abnormal growth in length and generally at the expense of the other two dimensions. In this instance the rule is reversed, and a similar case has been recorded by Kraus where the etiolated portion of the hypocotyl of a plant of *Lupinus Termis* was more than twice as thick as a normal hypocotyl. The shoot which develops from the plumule becomes the central upright stem of the plant.

Anatomy and Development of the Gynophore.

Longitudinal sections were made through young flower buds, at a stage before the formation of the egg in the embryo-sac, or at

least, before its fertilization. The bud at this stage is almost microscopically small. The ovary may be described as sessile, though there are a few layers of cells between its cavity and the place of insertion of the succeeding organs, the stamens. The basal or lower part of its cavity is nearly rectangular in shape; the ovules are attached to the parietal placenta by short stems. The bundles passing through the base of the ovary, or that part which may be considered the stem, number from 11 to 13. They extend through to the tip of the ovary, branching more or less in their course.

They consist of ducts with closely wound spiral markings, accompanied by very delicate elongated cells in which individual characteristics cannot be determined. There is also a certain cluster of cells lying near each bundle on the side toward the centre of the organ. They are so near the bundle as to suggest some functional relation with it. These cells are large, prismatic in shape and filled with an orange colored substance; they correspond to those occurring frequently in the Leguminosae, which are known as tannin cells.

After the egg is formed and fertilized the rudimentary stem begins to elongate and develop into the gynophore. The development of the young embryo was not studied, but the ovary itself remains nearly in the condition now described until the gynophore completes its growth. This may be seen from the fact that it does not increase perceptibly in size, but its extreme tip elongates slightly and is sharpened to an almost hair-like point. While the anatomy of the gynophore corresponds to that of the stem of any herbaceous dicotyledon, its manner of development resembles that of ordinary roots, as there are no lateral appendages and consequently no internodes.

The cluster of meristematic or dividing cells which give rise to it consists of those lying just below the ovary. For convenience in description we may divide this cluster into three parts: first, those cells which give rise to the central cylinder and which lie immediately below the cavity of the ovary; second, those producing the bundle cylinder, and lastly, those outside both of these, which form the rind tissue, or the hollow cylinder outside the bundles.

The first class consists of several layers numbering from ten to twelve cells in diameter. The first division occurs in the second layer under the cavity, anticlinal walls being formed, but with no great regularity. Soon afterwards the cells lying about the circumference of the upper layer begin to divide, forming new walls in such a manner as to change the rectangular shape of the lower portion of the cavity, that is, the angles or corners become filled with cells and the whole cavity assumes the oval form which it has at maturity. From this time on the several layers below the ovary divide rapidly by the formation of anticlinal walls; the cells so derived constitute the pith.

It will be understood from the nature of the case that the second part of the meristematic cluster, or that giving rise to the bundle cylinder, consists of the elements of the bundles already present. These bundles form an almost unbroken ring around the cavity of the ovary and have already been described as extending through it to its extreme tip. It is easy to determine what part of the bundles is in a formative or meristematic condition by the immature appearance of the ducts and the extremely thin walls of all the other cells. Owing to the irregularity in the order of division of the cells forming the central cylinder it is not possible to say definitely that the meristem of the bundle coincides in depth with that giving rise to the central cylinder. It is, however, highly probable that such is the case.

The third part of the meristematic cluster, or that lying outside the bundle ring, is so irregular in its division that no definite limits can be fixed. It is easier to distinguish the new walls here than in the tissues of the bundles. They appear to arise with no order. It can only be said that the cells of the zone lying next the meristem of the central cylinder are capable of growth and division, and that they form new cells rapidly enough to keep pace with the growth within.

Anatomy of the Mature Gynophore.

Two distinct parts may be recognized in the completed gynophore: that above ground with a smooth even surface, and that below, whose surface bears the hairs. The surface of the aerial portion is flecked with numerous lenticels which open length-

wise. The epidermal cells of the aerial portion show, on a cross section, a nearly oval lumen with a longer tangential diameter. A long section shows the length of the cells to be about three times their tangential diameter. All the walls are slightly thickened. These cells are interrupted by occasional stomata occurring about three to a square millimetre.

The rind, or that part of the ground-tissue extending between the epidermal layer and the bundle-cylinder, is about eight cells in depth. These cells are thin walled, of a nearly circular appearance, seen in a cross section, and with frequent intercellular spaces. In a long section their length is seen to correspond with the epidermal cells.

About half way between the epidermis and the bundle-cylinder a row of cells of peculiar character occurs. They appear to have a much longer tangential than radial diameter. But on examining them carefully they are seen to be completely plasmolytic, the radial walls lying in folds, which gives the appearance spoken of above. This row of cells was constant in the sections of the aerial portion of the gynophores examined. This circumstance is extremely puzzling, as no explanation can be offered for the phenomenon of plasmolysis in cells so situated.

The bundles are arranged in a circle according to the type of dicotyledonous stems. Through the greater part of the length of the gynophore they are constantly thirteen in number, but at either end, that is near the fruit or near the stem, they vary from this, numbering sometimes more and sometimes fewer. The circle of bundles with the tissue between them may be described as a hollow cylinder enclosing the pith. The individual bundle is covered toward the periphery by a partial sheath which extends laterally no further than the bast. This sheath is composed of one layer of cells which are smaller than the cells of the parenchyma of the rind and nearly isodiametric, and their anticlinal walls are frequently oblique.

The outline of the bundle itself, as seen on a cross section, is oval with the smaller part toward the centre. The outer part of the bundle is occupied by a heavy cluster of bast cells, which is convex toward the rind and slightly concave on its inner side. The remaining elements of the phloem were not distinctly made

out. The cambium consists of three or four layers of cells in depth, with nothing to distinguish it from cambium of ordinary collateral bundles.

The elements of the xylem are arranged according to the normal type. Following these elements radially from the cambium, first are found one or two reticulated ducts; after these come from one to several with annular markings; after these and next to the pith are one or two marked spirally. All of these ducts are very small in diameter; no porous ones were found. The libriform tissue is not well developed, the walls being hardly thicker than those of the surrounding parenchyma. Surrounding the reticulated ducts are small wood-parenchymatic cells.

It has already been said that the bundles are collateral and open. This statement requires some modification, as in the older portion of the organ the cambium of the bundles is no longer evident, its place being taken by differentiated phloem elements.

There is also an indication of the formation of a cambium ring. Such a ring never really occurs even in the oldest portion of the organ; but the bundles continue to develop both phloem and xylem elements until the ordinary method by which herbaceous stems accommodate themselves to this growth is no longer sufficient. This method, namely, the dilatation of the cells lying near the bundles, is beautifully illustrated here by the extreme size of the cells between the bundles. In the early stage of their development they are no larger than the cells of pith or rind, but as they become older they increase rapidly in both tangential and radial diameter.

This process, however, appears insufficient to keep pace with the growing cambium, and they now become meristematic, forming new walls which are at first tangential; later, radial walls are formed. In this manner arise clusters or bands of relatively small cells, extending from bundle to bundle. While these small cells appear like the ordinary meristematic tissue of stems whose cambium ring is formed after the bundles appear, they do not continue meristematic; at least, in the organs studied there was little evidence that these small cells produced lasting tissue of any kind, and none whatever of the formation of phloem and xylem elements. One or two other variations from the common type of dicotyledonous

stems may be mentioned. For example, near the base of the organ, that is, near the point of its attachment to the stem, the cells described as dividing to form the small cells are like those of the pith, as shown by the markings of their walls. They lie also in such a position as to indicate their connection with the pith rather than the rind cells. Owing to this, the bands which they form appear to connect the xylem parts of the bundles rather than the cambium layer.

At the other extremity, or near the growing region, this is not so evident, though the beginning of the division of these cells was found in a section one centimeter from the fruit.

Near the inner extremity of each bundle is a group of cells which have been referred to above as resembling the tannin cells of the family Leguminosae. There are usually several of these in a cluster, so arranged as to form a semicircle in the transverse section, whose concave side is toward the bundle. In the long section they lie in continuous rows. They correspond in size and shape to the larger pith cells, and are conspicuous on account of their deep brownish-yellow color.

The pith is composed of cells which appear circular in a cross section, and in a long section are seen to be somewhat elongated like the other cells of the ground system. The cells composing the outer edge of the pith are of about the same diameter as those of the rind tissue, but they increase in size as the centre is approached. They are provided with numerous pores on the radial and periclinal walls; these are linear or slit-like, and are arranged with their long diameters running obliquely from right to left. On the anticlinal walls, instead of pores, markings very similar to those of reticulated ducts occur.

The anatomy of the subterranean part of the gynophore differs from that above ground in the following respects: (1st) Most of the epidermal cells grow out into long hairs. (2nd) A growth in thickness occurs by a process similar to that of periderm formation, by which the diameter of the subterranean part is considerably increased. (3rd) By the absence of plasmolytic cells in the rind described above.

Nearly all of the epidermal cells develop long thin-walled one-celled hairs. These average about .8 mm. in length and are

from .002 to .02 mm. in the other two dimensions. They are slightly enlarged at the base, roundly obtuse at the end and filled with granular contents. No stomata were discovered in the underground portion, but their place was supplied by numerous lenticels.

The examination of a number of sections through this underground portion showed a row of phellogen cells extending around the stem, interrupted more or less in its regularity by frequent lenticels. Over that part of the surface where no lenticels occur three layers of cells had originated from the phellogen layer. By taking sections through a gynophore which has only begun to develop hairs, it is seen that this phellogen layer is the first layer of cells under the epidermis. The order of its development was not definitely determined, though there were indications that the first division was centrifugal and the two following centripetal. The diameter of the organ was thus increased by several layers of cells, as well as by the outward growth of the numerous lenticels. This latter fact also accounts for the unevenness of the surface of the subterranean portion. The cells derived from the phellogen retained the characteristic form and appearance of periderm. On testing for suberin, however, they were found to be entirely free from it, even in the older portions, when the hairs were beginning to die and separate from the cells below.

The cambium of the bundles throughout this portion was generally in an active condition, though it is not possible to state the exact portion of the organ where they lose their meristematic nature and change into phloem elements.

Experiments with the Hairs of the Gynophore.

Repeated experiments were made with plants bearing young gynophores which had not yet reached the ground when the plants were pulled up. Some were placed in a moist chamber and kept in the light; others were kept in darkness. In every case a narrow zone of hairs appeared in the course of about a week. This zone averaged three millimeters in length; its distance from the tip varied. On gynophores of stems kept in moist chambers in the light it was about eight millimeters; on those rolled in newspaper and kept but slightly moistened the zone of hairs was about one millimeter from the tip.

Schwarz states of his experiment with *Pisum sativum* that the hairs arising on the roots of plants raised in damp sawdust appeared between eight and thirteen millimeters from the tip, while those appearing on a plant of the same kind raised in dry earth, which offered more resistance than the sawdust, appeared from three to four millimeters from the tip.

In comparing the growth of gynophore hairs with that of root hairs it must be remembered that the growing point of the gynophore corresponding to the punctum vegetationis of the root lies just below the ovary which occupies the extreme tip of this organ. The ovary, however, is almost microscopically small and remains so during the growth of the gynophore. To illustrate the extremely small space occupied by it, the hairs which were not more than one millimeter from the tips of the gynophores as mentioned above were still below the growing point under the ovary. While this difference in the position of the growing point exists between root and gynophore, the difference which it makes in estimating the relative distances of the hairs from the tips is practically nothing.

The resemblance between these hairs and those of roots was further tested by repeated experiments in pulling young gynophores carefully from the soil. The minute portions of earth clung to the hairs and refused to be separated from them in the same manner as in the case of root hairs. In several instances these hairs were tested for acids and were found to respond readily to the litmus paper test.

Still another experiment was made which furnishes strong evidence that one function of the gynophore hairs corresponds to the chief function of those of the root. A large, well developed, thriftily growing plant was cut in such a manner as to separate the whole root system from the stems, but the latter were still connected with the ground by numerous well grown gynophores. The result was that the plant so treated after two weeks still presented nothing to a superficial inspection to distinguish it from others in its vicinity whose roots were left intact. Closer examination showed that some branches were dead; but the majority were putting out new leaves which appeared quite as strong and healthy as any of those on similar plants in the vicinity which

were supported by roots. Unfortunately these experiments were begun late in the season, and the appearance of the frost prevented their continuance.

It is hoped that in a future and more prolonged study of this plant, numerous and varied experiments of this nature will furnish additional proof of the conclusion reached above, namely, that the principal function of the gynophore hair is to furnish a supply of food material for the use of the developing fruit. It is hardly necessary to add here that if the secondary function of the root hair is to hold that part of the root on which it grows firmly, and so to facilitate the penetration of its tip into the soil, the same function must also be ascribed to the hairs of the gynophore, as the conditions are the same in both cases.

Observations on the Root.

On the germination of the first seeds planted for study it was noticed that there was a rupture of the epidermal cells, extending around the circumference of the root at the line where it joined the hypocotyl. The layer of cells so broken curved backward from the place laid bare, showing that it had been subject to a positive tension exerted by the underlying layers, which was strong enough finally to produce the rupture. The portion of the root so exposed grew rapidly and turned a slightly yellow. It was thought at first that this peculiar conduct might be due to the abnormal circumstances under which the seeds germinated, as they were planted in a box of moist sawdust in the laboratory. To test this, seeds were planted under all available differences of condition; some in greenhouses under glass, in sawdust; others in the same place, but in moist earth. Seeds were planted in the open air in various localities referred to at the beginning of this article, but always with the same result. As soon as the seed began to germinate, the break in the epidermis appeared. A study of the development of the young embryo was then undertaken with the following results: The embryo in the seed was found to have a normally developed primary root. The disposition of its meristems corresponds to that ascribed to the roots of the Leguminosae. After germination the dermatogen ceases to develop new cells, while the other meristems continue to divide, the outer lay-

ers of the periblem, tissue taking the place of an epidermis. As growth continues it appears that the outer layers do not keep pace with the inner, and cells of the surface are continually peeling off in rows or single layers many cells in length.

A cross section of a young root shows the outer layers of cells separating from the inner tissue and from each other by large intercellular spaces, and individual cells may be seen entirely isolated. In this view the peripheral three or four layers of the tissue of the cortex appear as an irregular zone, several cells deep, composed of cells which resemble the rest of the rind cells in shape, but which are much smaller.

These cells are thin walled like the remaining rind parenchyma, and are distinctly cutinized around their whole circumference. Thin sections as well as masses were placed in concentrated sulphuric acid. It was found that the walls of an outer portion, composed of these cells described, turned brownish yellow and remained intact, while the rest of the tissues of the parenchyma disappeared in a few hours. This cutinized portion was from two to three cells deep. The walls of the outer cells were entirely cutinized, while those of the cells next below these were cutinized on the side toward the circumference only.

The lateral roots show the same peculiar lack of epidermal tissue and, of course, no hairs appear. In other respects their anatomy resembles that of the ordinary dicotyledonous root. As they increase in age their outer surface is supplied with a regular periderm, and it is only in the early stages of growth that this peculiar habit may be observed.

Biological Considerations.

As the plant is only found under cultivation, at the present day, it is impossible to estimate in what degree its habits may have been influenced by its artificial surroundings. If, however, the changes induced by cultivation are generally in the direction of the inherent tendencies of the plant, emphasizing rather than changing such tendencies, the fact of cultivation would not enter largely into the question of the biology of *Arachis*.

The question of the course of the downward direction of growth of the gynophore has been answered by Charles Darwin,

in his work on "The Movements of Plants." He says that while apheliotropism may act in some slight measure, geotropism is unquestionably the exciting cause of the downward movement. He gives as proof of this the fact that gynophores grew straight down when the light in the greenhouses entered from one side as well as from above. His conclusions were corroborated by the experiments with the gynophore hairs already described, as they served at the same time to exhibit the geotropism of the downward movement. The light came to these plants through one window at the side. When the tips of the gynophores were pointing downward, the position of the stems was so changed as to reverse the direction of the tips, causing them to point directly upward. In a very short time a curve was formed in the growing portion of the gynophore, just below the apex, bringing the tip again to its former position, that is pointing directly downward. There were also some slight indications of a tendency of these organs to curve away from the light.

Darwin also refers to the means by which the organ is enabled to force its tip into the ground and make its way through it. The sharp, smooth point of the gynophore, he says, would probably enable it to penetrate the ground by mere force of growth, but its action is aided by a circumnutating movement. In evidence of this, he gives the result of a number of observations where circumnutation plainly took place.

By the study of its anatomy several other interesting facts have been obtained. First, the arrangement of the vascular tissues is such as to point clearly to its adaptation to the movement of the organ. The bundles, as before stated, run singly throughout its whole length. Furthermore, they lie close together and are characterized by heavy bast strands. The bast serves to strengthen the gynophore while pushing its way into the soil; at the same time pliability is given by means of the separate bundles which allow a freedom of motion not possible when there is a continuous ring.

Another and much stronger feature is unquestionably that of the hairs which form near the tip of this organ whenever and wherever it reaches the ground and has projected its tip into it for a slight distance. By this means the part of the organ already

grown is held firmly, while the growth near the apex forces the tip further and further into the soil.

In conclusion, it remains to be considered how much the facts ascertained in this study contribute to the solution of the question undertaken.

The fact that so many of the Leguminosae seek the ground in order to develop their fruit and that such different methods are employed in the accomplishment of this result must be regarded as having some important significance.

Tschirsch in an article on the root tubers of the Leguminosae, in the *Berichte der Deutschen Bot. Ges.* 1887, states that one group of nitrogenous compounds produced by the Leguminosae can be formed only in darkness and suggests this as a reason for the subterranean fruit of so many species of this order. This explanation does not answer the question satisfactorily, as *Trifolium subterraneum* plainly seeks to place its fruit under ground, and yet may both ripen and germinate it above ground. Beyond this the statement that some nitrates can only be formed in darkness does not meet with the concurrence of all authorities. It has also been suggested that the subterranean development of fruit is to enable it to avoid the danger of being eaten by grazing animals. These are the only reasons which have been offered in explanation of this phenomenon.

In reviewing the results obtained in this study, three facts stand prominently forth: namely, the absence of hairs on the root, the presence of hairs on the gynophore which may perform the chief function of root hairs, and lastly, the increased size of the subterranean part of the gynophore caused by a growth similar to that producing periderm.

While these facts alone are by no means sufficient to account for the underground development of the fruit they may at least furnish some evidence as to what is accomplished by this process. That the plant is able to take up water from the soil by means of the gynophore hairs was shown in the experiment where the roots were severed from the stem. The most puzzling feature in the anatomy of the gynophore is that of periderm formation in the portion under ground. In the large number of gynophores examined this was a constant feature of the subterranean portion,

and it was never found in the part above, except as it may be considered represented by the lenticels.

As the walls of the new cells are never suberized it may be suggested that one possible reason for their formation is to increase the number of cells near the surface, where the water from the soil comes in through the hairs. Their small size, however, seems to refute this idea, and even were it admitted as a reason it would not account for the increase of cells occurring only below ground.

Why do they not increase during the entire length of the organ, and thus present a normal condition agreeing with the typical stem? Whatever may be the answer to this question, the increase in the number of cells *does* furnish an additional reservoir of some considerable size for the water flowing in from the hairs.

In regard to the roots it is a well-known fact that the few Angiosperms that are known to be without root hairs are either plants which grow from bulbs and, therefore, do not require much nourishment from the soil, or water plants whose epidermis takes the place of root hairs, or epiphytes which also have no use for these organs. *Arachis* differs from all of these, not only in its need of food from the soil, but in the fact that it lacks both root hairs and a normal epidermal covering on those portions of the root where the hairs should develop. This latter fact points to the possibility that through this it has lost the power to produce hairs, which at one time belonged to its ancestors.

If this be true, the purpose of the gynophore cannot be simply to secure more nourishment than can be supplied by the roots, for they have *lost the habit* of forming hairs, showing that no great demand for food supply has been made upon them. If the plant does not require more nourishment from the soil than might be supplied by root hairs and yet forms such hairs on the gynophore instead of the root, we are forced to the conviction that for some reason it is advantageous to it to take its supply of food from the gynophore rather than the root. What reason can there be but one which has for a motive the welfare of the seed?

It has already been suggested that the plant needs to secure its seeds against the danger of being eaten by grazing animals. If this were in fact the purpose it may be seen how the conditions discovered facilitate its accomplishment. The fruit is not developed

until some time after the gynophore has reached the ground. The entire growth after the flower is formed is very rapid. If the fruit were first formed before a growth which pushed it under ground took place the chances for its safety would be much lessened. The fleshy cotyledons are both nutritious and pleasant to the taste and the seed is a favorite with many animals. The foliage of the plant is itself rich in nutritive properties and it is known to enrich the soil when used as a fertilizing agent.

If this were destroyed before the seeds were formed even after the ovaries were buried in the earth, the fruit could not perfect its growth unless provision were made whereby it could obtain and assimilate nourishment without the assistance of the leaves. Light is not necessary to the formation of proteids, and there is no reason to suppose that they may not be formed in an organ without leaves, if the necessary carbohydrates and nitrates are furnished.

The pith and other parenchymatic cells of the gynophore are stored with starch, and nitrates are obtained through the hairs. Therefore it is possible that if a growing seed were suddenly cut off from its normal supply of food by the destruction of the foliage, it would still be able to obtain a sufficient quantity to ripen it from the supplies in the gynophore.

The results so far obtained can only be taken as indications in favor of the second of the two hypotheses before mentioned. It is believed that actual proof, either for or against this hypothesis, may be obtained by a series of physiological experiments.

It is the intention of the writer of this paper to undertake such a series of experiments in the immediate future, believing that the results already obtained are such as to warrant the effort to carry the subject to a more satisfactory conclusion.

Explanation of Plates.

(PLATE 83.)

Fig. A. Portion of longitudinal section through the ovary of a young bud, showing cells bordering the lower side of the cavity of the ovary.

B. Diagrammatic drawing of the same section; x-y corresponds with x-y in A.

C. Portion of longitudinal section through the ovary of the flower showing the beginning of the gynophore growth. The rectangular appearance of the cavity of the ovary has already disappeared. (Compare with A.)

D. Portion of a longitudinal section through the ovary after the falling off of the calyx. Next stage to C. Corresponds to A. N. of C.

E. Portion of cross-section through the aerial part of a mature gynophore; a, a row of plasmolytic cells.

F. Ovary with style still attached.

(PLATE 84.)

A and B. Portions of cross-sections through the underground part of a gynophore, showing first division of phellogen layer at a. In A is seen the beginning of hairs at b, c and d.

C. Portion of cross-section of subterranean part of gynophore, showing at a the dilatation and division of cells of ground tissue lying between the bundles.

D. Portion of cross-section of the root, showing the zone of cells about the circumference, marked sec. in fig. E; a is a cell which has entirely separated and a portion of its length is seen.

E. Diagrammatic drawing of a segment of a cross-section of the root. The wood, zone is shown at x.

(PLATE 85.)

A. Showing hairs coming on a gynophore of a stem placed under a bell jar. After this gynophore was pointed downward the position of the stem was reversed so that the tip of the gynophore pointed upward. It is shown in the figure as it appeared when again pointing downward. The zone of hairs is seen at a.

B. A segment of a cross-section of gynophore, showing the hairs.

C. Diagrammatic drawing of a cross-section of the older part of a gynophore showing the proportion of bast in the bundle. Shaded portions represent bast.

D. A germinated seed showing at a the line of rupture of the epidermis of the root.

E. A gynophore with fruit just beginning to form. a—aerial part. b—subterranean part.

F. Gynophores bearing developing fruit.

G. A young gynophore which produced hairs while it was wrapped in a damp newspaper. a—zone of hairs.